Polydora and Related Genera as Borers in Mollusk Shells and Other Calcareous Substrates

(Polychaeta : Spionidae)

BY

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(4 Text figures)

INTRODUCTION

The boring activities of worms in the shells of mollusks were first described by naturalists in the eighteenth century. As early as 1737, Swammerdam noted that *Littorina* shells were eroded by small worms. In 1765, Baster described a species of "Nereis" from shells of oysters and other mollusks. The genus of worm involved in these reports and others was named *Polydora* by Bosc in 1802. Bosc's species, named *Polydora cornuta,* became the type of the genus but was too poorly described to permit subsequent identification and today is indeterminable. *Leucodore* Johnston, 1838 is a synonymous name that was in common usage during much of the nineteenth century.

Three genera, *Polydora, Boccardia,* and *Pseudopolydora* are today recognized within the polydorid complex. Each genus contains species capable of boring and will be considered in the present paper.

Polydorids are polychaetous annelids of the family Spionidae. Genera of the polydorid complex are the only spionids capable of boring. The mechanism of this boring has been the subject of considerable speculation over the years. The boring activities of polydorids result in simple U-shaped burrows, complex branching burrows, shallow depressions, or mud-blisters. Mud-blisters are the result of the worm's boring activities, accumulation of silt and reaction of the bivalve to the worm.

Several species of *Polydora* are able to damage mollusk shells by their boring activities. Because of the economic implications of polydorid infestations in commercially important bivalves, several species of *Polydora* have received considerable study. Those species most often recorded from shells of bivalves are *Polydora ciliata* (Johnston, 1838), *P. hoplura* Claparède, 1870, and *P. websteri* Hartman, 1943. Other species from mollusks of no commercial importance have, on the other hand, received little attention. What records there are of such associations are widely scattered throughout a voluminous literature. Attempts to review this literature have generally dealt only with those species which penetrate commercially important bivalves. During the course of studies by the two of us on different aspects of *Polydora* biology, it became apparent that a published summary of this large literature would be useful.

It is the purpose of the present paper to summarize the known records of polydorids which penetrate calcareous substrates. Subsequent papers will deal with new investi-

[1] Contribution No. 31 from the Pacific Marine Station; Contribution No. 94 from the Marine Sciences Research Laboratory of the Memorial University of Newfoundland; and Contribution No. 288 from the Biology Department of the Memorial University of Newfoundland

gations currently in progress on burrow patterns, specificity of attack, infestation rates, larval development, and taxonomy of polydorids from various calcareous substrates.

MOLLUSCAN INFESTATIONS

Part A: Bivalvia

Several species of *Polydora* are known to damage the shells of bivalves. They are especially well known as pests of the oyster and scallop industry. For this reason the literature describing their associations is large and extends back more than a hundred years.

The harmful effects of *Polydora* on the host species vary with the intensity of infestation and the type of burrow formed. The burrow type, as reported by many authors, is constant under the specific conditions they describe. However, on a global basis, the form of the burrow appears to bear little relation to the species of *Polydora,* the species of the host, or even the geographical location.

Burrow Types

Three main types of *Polydora* burrows have been described on bivalve shells: 1) Surface fouling; 2) U-shaped burrows; 3) Mud-blisters.

Surface fouling occurs when *Polydora* settle on a surface but do not penetrate. The worms accumulate a thick layer of mud around themselves and over the surface of the substrate. The individual worms extend their burrows beyond this mat as 2 neat, round, mud-colored tubes. Through these tubes the head or pygidium emerge.

The European species, *Polydora ciliata,* is an important surface fouler both on subtidal harbor structures (Persoone, 1965) and on European oysters (Korringa, 1951). *Polydora ligni* Webster, 1879 causes surface fouling of some American east coast oyster beds (Mortensen & Galtsoff, 1944; Galtsoff, 1964).

U-shaped burrows penetrate the structure of the shell. These burrows have a distinctive form which makes them easily recognizable as the work of *Polydora.* This burrow has been illustrated and described by numerous workers,

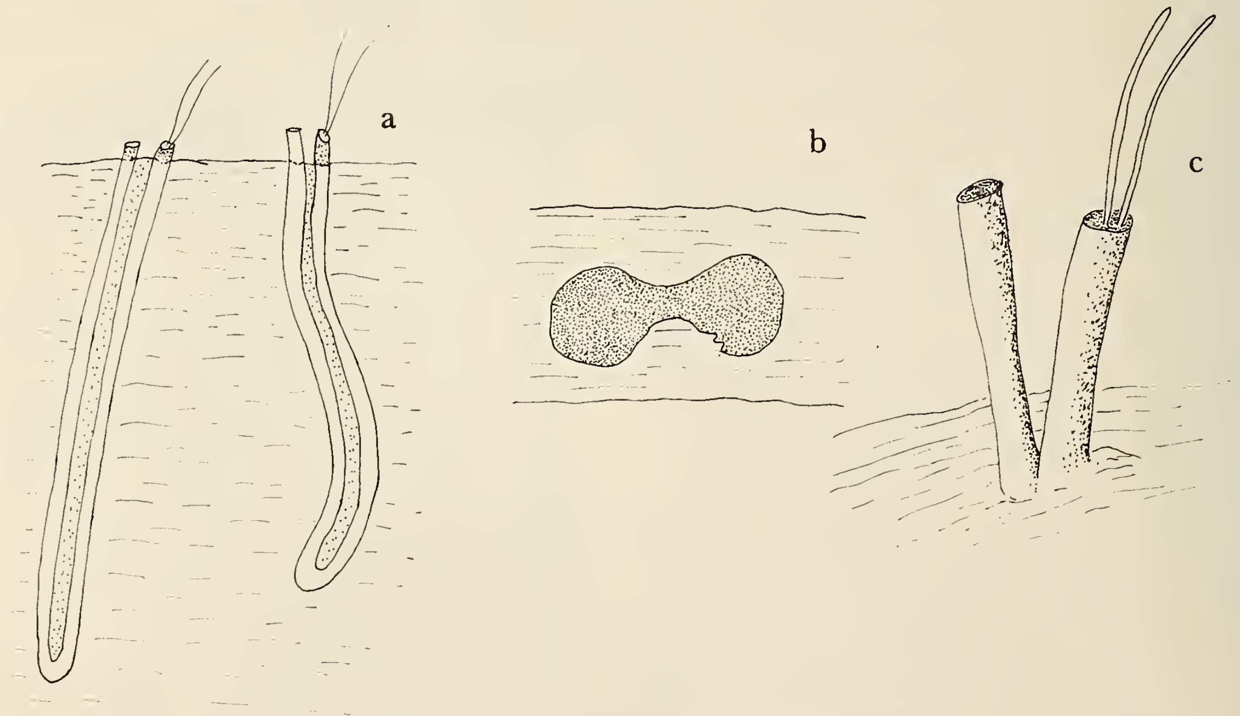

Figure 1

Basic structure of *Polydora burrow*
a: U-shaped burrow of *Polydora ciliata*
b: cross-section through burrow of *Polydora concharum* (after Evans, 1969)
c: external silty extensions of *Polydora* spp.

including Lamy & André, 1937; Davis, 1967; and Evans, 1969. It consists of an elongated U with the arms of the U being parallel and quite close together (Figure 1a). The worm lies rather loosely within the U. The space between arms is open but narrower, so that a cross section looks like a broad-centered figure 8 (Figure 1b). Most authors report that the burrow is a simple unbranched U, but Seilacher (1969) and Evans (*op. cit.*) describe burrows which branch repeatedly (Figure 3h). The ends of the burrow are extended by short mud-colored tubes which give the outside of the shell a hairy appearance.

Mud-blisters have been described by many authors, including Whitelegge (1890); Lunz (1941); and Korringa (1951). They are masses of mud accumulated on the inner surface of the shell by the recently settled *Polydora*. The host reacts first by secreting over the mud a roof of conchiolin and later a layer of nacreous material (Figure 2). The worms occupy the mud-filled chambers so formed and communicate with the exterior via pairs of tubes either at or close to the periphery of the shell. This is the most damaging effect of *Polydora* on bivalves.

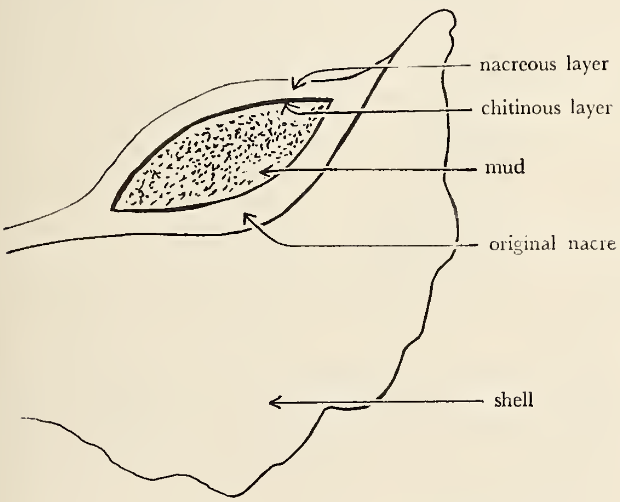

Figure 2

Diagrammatic section through shell of oyster and mud-blister (after Lunz, 1941)

Paleontological Occurrence

Both U-shaped burrows and mud-blisters are found in fossil shells.

The Treatise on Invertebrate Paleontology (Moore, 1962) described U-shaped boring tunnels, that look like *Polydora* burrows, called *Caulostrepsis* (Clarke, 1908) = *Polydorites* (Douville, 1908). These are found in shells of brachiopods, echinoids and mollusks from the Lower Devonian, Upper Triassic, and Tertiary.

Lunz (1941) reported mud-blisters in *Crassostrea virginica* (Gmelin, 1791) from Florida fossil beds, probably of the Pleistocene period.

Davis (1967) described the presence of the typical U-shaped "*Polydora*-type" burrows in the wedge clam, *Mesodesma arctatum* Conrad, 1830, from the Pleistocene in Maine.

Boekschoten (1967) reported the presence of *Polydora* burrows, both U-shaped and mud-blisters, in clam and oyster shells from the Tielrode Sands (Pliocene, Belgium). *Polydora* is found in *Cardium edule* Linnaeus, 1758 from the Wadden Sea (Boekschoten, 1966).

Cameron (1967; 1969) reported a Devonian fossil worm, *Vermiforafacta rollinsi* Cameron, 1967, which lived in a slightly curved, cylindrical burrow in the shell of a bivalve. He claimed that the worm resembled living members of the family Spionidae in form and habit. The circular cross section of this burrow, however, is quite unlike that of any known, living, shell-boring spionid.

Living *Polydora* and *Boccardia* that Form Associations with Bivalves

In European waters *Polydora ciliata* and *P. hoplura* are important pests of the oyster *Ostrea edulis* Linnaeus, 1758. There appears to be considerable disagreement in the literature concerning the tube-building behavior of these 2 species. Carazzi (1893) and Dollfus (1921) observed that *P. ciliata* formed mud-blisters in the oyster, the larva settling between the mantle and the edge of the shell. Dollfus also made the unlikely claim that *P. ciliata* occasionally bores cylindrical tunnels. Lamy & André (1937) and Korringa (1951) stated that *P. ciliata* forms U-shaped burrows. The latter author also observed that this species causes surface fouling.

Dollfus (1921) and Lamy & André (1937) claimed that *Polydora hoplura* forms U-shaped burrows in the oyster shell. The former author also claimed that this species forms mud-blisters by penetrating through the shell.

Korringa (1951) strongly presented the idea that *Polydora hoplura* and *P. ciliata* differ primarily on a behavioral basis in that *P. hoplura* only forms mud-blisters while *P. ciliata* only forms surface mats of U-shaped tunnels. He even extends this generalization to "biologically related" North American (*P. websteri*) and Australian (*P. ciliata*) mud-blister forming polydorids and suggests that these forms are actually more closely related to *P. hoplura*.

Table 1

Host, Geographical Location, and Burrow Type of *Polydora websteri*

Author and date	Host species	Burrow Type	Geographical Area
Kavanagh, 1940	*Crassostrea gigas*	mud-blister	Gulf of Mexico
Lunz, 1940, 1941	*Crassostrea virginica*	mud-blister	South Carolina
Needler, 1941	*Crassostrea virginica*	mud-blister	eastern Canada
Loosanoff & Engle, 1943 (includes Hartman's original description)	*Crassostrea virginica*	mud-blister	New England
Hartman, 1945	*Crassostrea virginica*	mud-blister	North Carolina
Frey, 1946	*Crassostrea virginica*	mud-blister	Potomac River
Medcof, 1946	*Crassostrea virginica*	mud-blister	eastern Canada
Hartman, 1951	"mollusc shells"	U-shaped tubes with mud blisters	Gulf of Mexico
Mackin & Cauthron, 1952	*Crassostrea virginica*	mud blister (?)	Gulf of Mexico
Owen, 1957	*Crassostrea virginica*	U-shaped tubes which may become mud blisters	
Hopkins, 1958	*Crassostrea virginica*	U-shaped tubes with mud blisters	Gulf of Mexico
Turner & Hanks, 1959	*Pecten irradians*	mud-blister	New England
Hartman, 1961	*Ostrea lurida* & *Patinopecten caurinus*	U-shaped burrows and mud blisters	California and Oregon coasts
Wells & Wells, 1962; Wells *et al.*, 1964	*Aequipecten gibbus*	mud-blister	North Carolina
Galtsoff, 1964	*Crassostrea virginica*	mud-blister	New England
Hartman, 1966	*Crassostrea virginica*	?	Hawaii
Davis, 1967	*Mesodesma deauratum*	U-shaped burrows	Gulf of St. Lawrence
Forbes, 1966	*Ostrea permollis*	mud-blister	Florida-Gulf of Mexico
Landers, 1967	*Mercenaria mercenaria*	mud-blister	New England
Blake, 1969a, b; 1971	*Placopecten magellanicus*	U-shaped burrow	Maine
Evans, 1969	*Placopecten magellanicus*	U-shaped burrow	Newfoundland
unpublished	*Mytilus edulis*	U-shaped burrow	Newfoundland
unpublished	*Modiolus modiolus*	U-shaped burrow	Newfoundland
unpublished	*Hinnites multirugosus*	U-shaped burrow	British Columbia

Whitelegge (1890) and Roughley (1922) described attacks of the mud worm *Polydora ciliata* on the Australian oyster *Ostrea cucullata*. In this area *P. ciliata* forms large and numerous mud-blisters which often lead to the death of the oyster.

In North American waters *Polydora websteri* is the most important pest species. This species is very similar to *P. ciliata* and prior to Hartman's (1943) description and renaming it was known by that name. Table 1 summarizes the host invaded, types of burrows formed and geographical location of *P. websteri* attacks. It will be noted that in all cases except *Mercenaria mercenaria* (Linnaeus, 1758) the bivalves attacked are surface dwelling or very shallow burrowing forms. The young *M. mercenaria* described by Landers (1967) were attacked because they were unable to burrow into soft substrate. In 1969, the second author collected large dead *M. mercenaria* on a beach near Redbank, New Jersey. These shells were bored by typical U-shaped *Polydora* burrows similar to those formed by *P. websteri* in *Placopecten magellanicus* (Gmelin, 1791) (Evans, 1969). These borings were probably made after the death of the clam when the shells were lying on the surface of the sand.

Polydora websteri infestations of *Crassostrea virginica*, *C. gigas* Thunberg, 1793, *Pecten irradians* Lamarck, 1819, *Aequipecten gibbus* Linnaeus, 1758, and young laboratory-reared *Mercenaria mercenaria* all cause the formation of mud-blisters. On the other hand, infestations of *Ostrea lurida* Carpenter, 1863 and *Patinopecten caurinus* (Gould, 1850) from the Pacific coast, of *Mesodesma deauratum* Turton, 1830 and *Placopecten magellanicus* from the Gulf of St. Lawrence and Newfoundland caused the formation of U-shaped burrows.

These observations would tend to contradict Korringa's concept of "biologically distinct" species in that *Polydora* *websteri* under different circumstances, does form 2 types of burrows.

Polydora ligni occurs on the Atlantic and Pacific coasts of North America. Usually it is free-living in mud (Galtsoff, 1964) or waterlogged wood (Hartman, 1945). However, it sometimes forms surface mats on oysters.

Nelson & Stauber (1940) reported that a worm tentatively identified as *Polydora ligni* occupied mud-blisters in the shells of oysters in Delaware Bay. There have never been any subsequent observations of *P. ligni* in mud-blisters so it is assumed that this was an erroneous identification; it was more likely *P. websteri.*

Polydora concharum Verrill, 1880, appears to have been very little discussed in the literature from a biological standpoint. Verrill (1880: 176) described it as "very common all along the coast from Cape Cod to Nova Scotia in 10 to 100 fathoms, in tortuous narrow galleries excavated in shells especially of *Cyprina islandica.*" No figures of these burrows were included in his description.

Evans (1969) describes and illustrates the burrows of *Polydora concharum* in the shells of the sea scallop *Placopecten magellanicus* (Figure 3h). Blake (1969a; 1969b; 1971) described the adults and larvae of *P. concharum.* He noted that the species occurs commonly in shells of living *Placopecten magellanicus* and dead shells of *Mercenaria mercenaria* in Maine waters.

Verrill (1880) described a new species, *Polydora gracilis* as living gregariously in shells of *Placopecten magellanicus.* However, he did not describe the burrow type. Blake (1969a) considers that *P. gracilis* may be a synonym of *P. socialis* (Schmarda, 1861). The latter species was reported by Blake (1969a; 1969b; 1971) as being a common borer in shells of living *Placopecten magellanicus* and old dead *Mercenaria mercenaria* in the Damariscotta Estuary of Maine. In a larval study, Blake (1969b) noted that *P. socialis* larvae metamorphose on both shell and sediment. Juveniles bore into a shell, excavate a burrow and commence gathering silt from the water and construct a silty tube which projects from the burrow. The burrows themselves have a tough mucoid lining.

Boccardia hamata (Webster, 1879) (formerly placed within the genus *Polydora*) was reported from bivalve shells by Webster (1879a; 1879b) from New Jersey and Virginia. Hartman (1951) and Hopkins (1958) reported the species from oyster shells from the Gulf of Mexico. Rioja (1960) reported *B. hamata* from the Lagoon of Mandina (eastern Mexico) from bivalve shells. Blake (1966) redescribed the adults and reviewed the literature of the species while Dean & Blake (1966) described the larval development on the east and west coasts of North America.

Pillai (1965) described *Polydora cavitensis* from oysters in the Philippines, but did not discuss the ecology of that species.

Blake & Woodwick (1971, 1972) describe 3 new polydorids, *Boccardia berkeleyorum, Polydora convexa,* and *P. elegantissima* from California bivalve mollusks. *Boccardia berkeleyorum* and *P. convexa* inhabit shells of *Pododesmus macroschisma* (Deshayes, 1839). They note that *P. convexa* forms branched burrows similar to those of *P. concharum* as reported by Evans from *Placopecten* shells. *Polydora elegantissima* occurs in shells of *Tivela stultorum* (Mawe, 1823)

Methods of Attack by Mud-Blister Forming Polydorids

The information available concerning the route of invasion followed by the mud-blister forming polydorids is contradictory (Table 2). A number of authors claimed that the larva swims into the mantle cavity or burrows between the mantle and shell where it begins to accumulate mud. The presence of the burrows away from the periphery is explained by the subsequent growth of the bivalve shell. Others observed that the larva settles on the outside of the shell, penetrates to the mantle and there forms the mud blister. It seems possible that both routes of attack could, under different circumstances, be followed.

Part B: Gastropoda

Polydorids are common inhabitants of gastropod shells. In particular, shells occupied by hermit crabs seem to offer a suitable habitat. In contrast to the extensive studies of polydorid infestations in bivalves, there has been little investigation of the heavy infestation often seen in this habitat. Little information is available on infestation by polydorids in shells of abalone (*Haliotis* spp.). Day (1967) mentions that *Haliotis midae* from South Africa is heavily infested with *Polydora.* In California, Hansen (1970) found that 11% of *H. rufescens* Swainson, 1822 and 12% of *H. cracherodii* Leach, 1817 were infested with polydorids. He noted that the burrows began in the area of the protoconch and subsequently spread to other areas of the shell.

Twelve species of *Polydora* and 5 *Boccardia* have been recorded from gastropod shells (Table 3). These scattered accounts come mostly from Europe and the west coast of North America, while a few records come from New England, North Carolina, and South Africa.

Published information on the biology of gastropod shell inhabiting polydorids suggests two distinct methods by

Table 2

Summary of Route of Invasion of Mud-Blister Forming *Polydora*

Author and date	*Polydora* species	Host species	Route of attack
Whitelegge, 1890	*Polydora ciliata*	*Ostrea cucullata*	Larvae swim into open oyster; fix by head to shell margin
Carazzi, 1893	*Polydora ciliata*	*Ostrea edulis*	Between shell and mantle
Dollfus, 1921	*Polydora ciliata*	*Ostrea edulis*	Swims into open oyster; attaches by head to shell margin
	Polydora hoplura	*Ostrea edulis*	Penetrates shell
Kavanagh, 1940	*Polydora websteri*	*Crassostrea gigas*	Creeps within shell cavity causing oyster to form blister
Lunz, 1941	*Polydora websteri*	*Crassostrea virginica*	Swims into open oyster; secures a favorable position and gathers mud around itself
Needler, 1941	*Polydora websteri*	*Crassostrea virginica*	Enters oyster when small; lies between mantle and shell
Medcof, 1946	*Polydora websteri*	*Crassostrea virginica*	Establishes itself between pallium and shell near margin; accumulates mud in which it lives; oyster produces blister by roofing mud with limy shell
Korringa, 1951	*Polydora hoplura*	*Ostrea edulis*	Larvae penetrate between oyster mantle and shell
Hopkins, 1958	*Polydora websteri*	*Crassostrea virginica*	Larvae settle on surface of shells and excavate U-shaped burrows which may be expanded to mud blisters when the shell is penetrated
Galtsoff, 1964	*Polydora websteri*	*Crassostrea virginica*	Larvae settle on external surface of young oysters and form shoe-shaped burrows near extreme edge of shell
Wells *et al.*, 1964	*Polydora websteri*	*Aequipecten gibbus*	Larvae insert themselves between mantle edge and shell
Landers, 1967	*Polydora websteri*	*Mercenaria mercenaria*	Larvae settle on outside surfaces of laboratory-reared hard clams; not found in natural populations

Table 3

Records of *Polydora* and *Boccardia* from Gastropod Shells

Species	Host Shell	Hermit Crab Present	Locality	Reference
Polydora bioccipitalis	*Ocenebra poulsoni*	yes	California	Blake & Woodwick, 1972
	Olivella biplicata	yes	California	Blake & Woodwick, 1972
	Murex gemma	yes	California	Blake & Woodwick, 1972
	Polinices reclusianus	yes	California	Blake & Woodwick, 1972
Polydora capensis	?	no	South Africa	Day, 1955, 1963
Polydora ciliata	*Littorina littorea*	no	Norway	Söderström, 1920, 1923
	Littorina littorea	no	Norway	Dollfus, 1932
	Littorina littorea	no	Germany	Ankel, 1936
	Littorina littorea	no	Sweden (Gullmar Fjord)	Hannerz, 1956
	Littorina littorea	no	Germany	Hempel, 1957
	Littorina littorea	no	Sweden (Øresund)	Eliason, 1920
	Littorina littorea	no	Denmark (Øresund)	Thorson, 1946
	Littorina littorea	no	Sweden	Orrhage, 1969
	Littorina obtusata	no	Germany	Ankel, 1936
	Buccinum undatum	no	Germany	Hempel, 1957
	Crepidula fornicata	no	Germany	Hempel, 1957
	Gibbula cincreria	no	Germany	Ankel, 1936
	Nucella lapillus	no	Germany	Ankel, 1936
	Neptunea antiqua	no	Sweden (Øresund)	Eliason, 1920
	Patella vulgata	no	Sweden (Gullmar Fjord)	Hannerz, 1956

Table 3 [Continued]

Polydora commensalis	*Nassarius obsoletus*	yes	North Carolina	ANDREWS, 1891a, b
	Nassarius obsoletus	yes	Eastern Canada	BERKELEY & BERKELEY, 1956
	Thais lamellosa	yes	British Columbia	BERKELEY & BERKELEY, 1936
	Thais emarginata	yes	California	WOODWICK, 1963b
	Lunatia heros	yes	Connecticut	HATFIELD, 1965
	Polinices duplicata	yes	Connecticut	HATFIELD, 1965
	Busycon canaliculatum	yes	Connecticut	HATFIELD, 1965
	Buccinum undatum	yes	Connecticut	HATFIELD, 1965
	Littorina littorea	yes	Connecticut	HATFIELD, 1965
	Littorina littorea	yes	Maine	BLAKE, 1969a, b; 1971
	Olivella biplicata	yes	California	WOODWICK, 1963a, b
	Ceratostoma nuttalli	yes	California	WOODWICK, 1963b
Polydora convexa	*Tegula brunnea*	yes	California	BLAKE & WOODWICK, 1972
	Olivella biplicata	yes	California	BLAKE & WOODWICK, 1972
	Diodora aspera	no	California	BLAKE & WOODWICK, 1972
Polydora elegantissima	*Olivella biplicata*	yes	California	BLAKE & WOODWICK, 1972
Polydora hoplura	*Thais lapillus*	no	France	FISCHER, 1930
Polydora punctata	?	yes	El Salvador	HARTMANN-SCHROEDER, 1959
Polydora maculata	*Bullia laevissima*	yes	South Africa	DAY, 1963
Polydora pygidialis (as *P. ciliata*)	*Tegula funebralis*	yes	California	BLAKE & WOODWICK, 1972
	Thais lamellosa	yes	British Columbia	BERKELEY & BERKELEY, 1956
	Thais emarginata	yes	California	WOODWICK, 1963b
	Tegula brunnea	yes	California	WOODWICK, 1963b
	Tegula brunnea	yes	California	BLAKE, 1966
	Olivella biplicata	yes	California	WOODWICK, 1963a, b
	Acanthina spirata	yes	California	WOODWICK, 1963a
	Acanthina spirata	yes	California	BLAKE & WOODWICK, 1972
Polydora websteri	*Littorina littorea*	yes	Maine	BLAKE, 1969a, b; 1971
Boccardia berkeleyorum	*Tegula brunnea*	yes	California	BLAKE & WOODWICK, 1971
Boccardia columbiana	*Acanthina spirata*	yes	California	WOODWICK, 1963a
	Tegula funebralis	yes	California	WOODWICK, 1963a
	Tegula brunnea	yes	California	WOODWICK, 1963b
	Thais emarginata	yes	California	WOODWICK, 1963a
	Purpura foliata	yes	California	WOODWICK, 1963a
	Olivella biplicata	yes	California	WOODWICK, 1963a
	Diodora aspera	no	California	WOODWICK, 1963a
	Jaton festivus	no	California	WOODWICK, 1963a
Boccardia hamata	*Tegula brunnea*	yes	California	BLAKE, 1966
	Lunatia heros	yes	Connecticut	DEAN & BLAKE, 1966
Boccardia proboscidea	*Tegula funebralis*	yes	California	WOODWICK, 1963a
	Tegula brunnea	yes	California	WOODWICK, 1963a
	Acanthina spirata	no	California	WOODWICK, 1963a
	Jaton festivus	no	California	WOODWICK, 1963a
	Olivella biplicata	yes	California	WOODWICK, 1963a
Boccardia tricuspa	*Tegula brunnea*	yes	California	WOODWICK, 1963a
	Ceratostoma nuttalli	yes	California	WOODWICK, 1963a
	Olivella biplicata	yes	California	WOODWICK, 1963a
	Thais emarginata	yes	California	WOODWICK, 1963a

which they become established in the shells. The first and most common is where the worm first invades the outside of the shell and gradually erodes its substance. The one species which has been studied in this regard is *Polydora ciliata*. HEMPEL (1957) found that *P. ciliata* first attacked the sculptured areas of *Littorina littorea* Linnaeus, 1758 and *Buccinum undatum* Linnaeus, 1758. The larvae settled and perforated the seams from the outside with fine holes and in an advanced infestation eroded the entire apex. She did not find many of the burrows to penetrate the interior of the shell although ANKEL (1936) had earlier found that the umbilicus of *Gibbula cinereria* Linnaeus, 1758 was almost always inhabited by *P. ciliata*.

Most species of *Polydora* and *Boccardia* listed in Table 3 probably become established in the manner described by Hempel. *Polydora commensalis* Andrews, 1891, however, invades gastropod shells in an entirely different manner. *Polydora commensalis* is known only from shells inhabited by hermit crabs. This commensal relationship is not specific with regard to host shell or crab (HATFIELD, 1965; BLAKE, 1969a). Further, the species has been recorded from widely scattered geographical localities (Table 3). The external opening of a *P. commensalis* burrow occurs on the inner lip of the aperture of the shell as a conspicuous rounded hole (ANDREWS, 1891). This opening may or may not be visible from the outside of the shell (BLAKE, *op. cit.*). The burrow leads from the aperture in long passages around and within the columella (ANDREWS, *op. cit.*, HATFIELD, *op. cit.*), to the apex of the shell. For most of its length the burrow is a shallow depression, roofed over with a thin calcareous mass. It is not known if the worm secretes or redeposits the roof.

ORRHAGE (1969) found that *Littorina littorea* having a shell shorter than 10 mm were not infested by *Polydora ciliata* and that the snails do not become sexually mature until they have reached those dimensions. He suggests that larvae of *P. ciliata* may be guided to *Littorina* by some substance which the snails secrete into the water. However, he has no data to support the latter contention.

CORAL INFESTATIONS

Four species of *Polydora* and 3 of *Pseudopolydora* have been reported to bore into coral. OKUDA (1937) found *P. armata* Langerhans, 1880 living commensally with *Leptastrea purpurea* in Japan. WOODWICK (1964) reported 5 species from the Marshall Islands which were taken from coral. The species were *P. armata*, *P. tridenticulata* Woodwick, 1964, *Ps. corallicola* Woodwick, 1964, *Ps. reishi* Woodwick, 1964, and *Ps. pigmentata* Woodwick, 1964. LIGHT (1970a) described *Polydora alloporis* from central California. The species was found abundantly in burrows bored into the coenosteum of the hydrocoral *Allopora californica* Verrill, 1866. In a second paper, LIGHT (1970b) described *P. wobberi* from a white gorgonian, *Lophogorgia* sp., from Baja California.

There have been no studies on the biology of coral infesting species. HARTMAN (1954) suggested that *Polydora* and other annelids may have a destructive effect on reef building processes of corals or coralline algae.

Table 4

Polydora and *Boccardia* from Coralline Algae

Species	Alga	Locality	Reference
Polydora ciliata	*Lithothamnion*	France	MESNIL, 1896
	Lithothamnion	Sweden	HANNERZ, 1956
	–	California	WOODWICK, 1963b
Polydora giardi	*Lithothamnion*	France	MESNIL, 1896
Polydora armata	*Lithothamnion*	France	MESNIL, 1896
	Lithothamnion	Japan	OKUDA, 1937
	Prolithion oncodes	Marshall Islands	WOODWICK, 1964
Polydora flava	*Lithothamnion*	France	MESNIL, 1896
	Lithothamnion	Sweden	HANNERZ, 1956
Polydora caeca	*Lithothamnion*	France	MESNIL, 1896
	Lithothamnion	Ireland	SOUTHERN, 1914
Boccardia berkeleyorum	*Lithothamnion*	California	BLAKE & WOODWICK, 1971
Boccardia columbiana	*Lithophyllum*	California	WOODWICK, 1963a, b
Boccardia proboscidea	*Lithophyllum*	California	WOODWICK, 1963a, b
Boccardia tricuspa	*Lithophyllum*	California	WOODWICK, 1963a, b

INFESTATIONS OF CORALLINE ALGAE

At least 5 species of *Polydora* and 3 of *Boccardia* have been recorded from coralline algae (Table 4). MESNIL (1896) records 5 species of *Polydora* as occurring in coralline algae in France, but gives no information as to their mode of infestation or ecology. WOODWICK (1963a, 1963b) records *P. ciliata, B. tricuspa* (Hartman, 1939), *B. proboscidea* Hartman, 1940, and *B. columbiana* Berkeley, 1927 from *Lithophyllum* sp. The 2 former species produced clean burrows in the alga and were apparently true borers, while the 2 latter species, although able to erode the alga, were considered to be nestling forms.

DISCUSSION

Theories and Experimental Evidence Concerning Mechanisms of Shell Penetration by *Polydora*

The literature on this subject dates back well into the nineteenth century and includes ideas which have at times evoked considerable controversy among different investigators.

LANKESTER (1868) was the first person to treat the actual boring of a *Polydora, P. ciliata.* He did not believe that the heavy spines of the 5th setiger could in any way affect lime and concluded that the boring was accomplished by chemical means. He believed that an acid secretion was derived from segmental glands, later termed "poches glanduleuses" by CLAPARÈDE (1870).

MCINTOSH (1868) strongly disagreed with Lankester because the worm could be found in burrows in substrates other than calcareous, namely shale and sandstone. He thus favored mechanical penetration over a purely chemical mechanism.

WHITELEGGE (1890) studied *Polydora ciliata* in Australian oysters. He advanced the idea that the worm did not bore at all but instead that the larvae entered the oyster from the inside, attached themselves to the inside of the shell and there surrounded themselves with mud. The irritated oyster then deposited a layer of lime over the animal. This type of structure is what we call a mud-blister. Actually, HASWELL (1885) had earlier described similar blisters from Australian oysters, a work apparently overlooked by Whitelegge. MCINTOSH (1902) again disagreed with these findings, by pointing out that mud-blisters were not formed by the worms when they lived in other substrates and by the fact that very few British oysters have mud-blisters. In retrospect, it may well be that the apparent behavioral difference observed by these two authors for *P. ciliata* in Australia and Britain may be due to a taxonomic problem. Indeed, KORRINGA (1951: 97) has stated:

> "The most serious damage to the oyster industry in many parts of the world is imputed in the literature to *Polydora ciliata.* In practically every case presented *Polydora ciliata* could plead not guilty, and point to other members of the *Polydora* family as the culprits. I have not enough space here to clear up this confusion which is found in the literature on this point. It is enough to mention that *Polydora ciliata* most probably does not occur at all in America (Hartman, 1945), and Australia, from where its harmful effects have been reported.
>
> "Much of the havoc caused in many important oyster districts, and ascribed to *Polydora ciliata,* has in fact been caused by *Polydora hoplura* or by biologically closely related species like *Polydora websteri* Hartman. The latter species all show the same way of living differing from that of *Polydora ciliata.*"

Polydora hoplura and *P. websteri* are known to form mud-blisters in oysters while *P. ciliata* apparently does not. The first author has examined some of Haswell's material and has found that the specimens agree more closely with *P. websteri* than with *P. ciliata.*

Despite probable taxonomic problems, the controversy over mechanical versus chemical means of shell penetration continued into the early twentieth century.

SÖDERSTRÖM (1920) first emphasized mechanical abrasion by the heavy spines of setiger 5 as he observed *Polydora ciliata* through thin burrows. He demonstrated that the U-shaped burrow resulted from an originally undivided hole in which an intermediate wall of detritus, etc., was built up. He considered that the boring was a joint effect between the secretion of an acid by the "poches glanduleuses," and mechanical abrasion of the modified bristles of setiger 5. In a later paper (SÖDERSTRÖM, 1923) he changed his view by suggesting that the spines were merely a means of support or adhesion during ventilation or feeding and that the mechanism of boring was purely chemical.

In recent years the controversy of mechanical versus chemical boring has been revived.

HANNERZ (1956) in an elegant larval study noted that *Polydora ciliata* larvae possessed a pair of opaque gray glands ventral to the heavy spines in setiger 5. Although different in structure from the "poches glanduleuses," which in adults occur in segments 7, 8, and 9, he considered them homologous. Hannerz felt that these glands in the 5th setiger of larvae secreted a substance which facilitates the initial boring by the worm. He was also very impressed with the musculature associated with the specialized 5th segment and disagreed with Söderström's contention that the so-called bore bristles were primarily for adhering the worm in one position. Hannerz was of the opinion that boring involved both a chemical and a mechanical action on the material. A substance secreted by the glands converts the lime into a more easily workable substance which is later eroded with the help of the bristles. Since the described glands were exclusively larval, he contended that boring in adults was accomplished entirely with the aid of bristles.

Hempel (1957) determined that *Polydora ligni, P. quadrilobata* Jacobi, 1883 and *P. ciliata* bore into hard clay with the setae of the 5th segment. The burrows in clay were similar to those made by *P. ciliata* in calcareous material. From this information and from the fact that she saw scratches in new bore holes she determined that *P. ciliata* bores by mechanical means only. She noted as Hannerz had that the musculature of the 5th setiger was especially well developed and that the setae showed distinct signs of wear. Specimens kept in sand did not show setal wear as did those taken and allowed to penetrate shells.

Dorsett (1961) favored the view that both chemical and mechanical methods were used by the worms to bore. Although no specific acid was identified, the use of a sequestering or chelating agent linked with the biochemistry of mucus was suggested. He also noted the heavy musculature of the 5th setiger and observed the behavior of recently metamorphosed worms on clay.

The majority of this literature has dealt with *Polydora ciliata*. Haigler (1969) and Evans (1969), however, have dealt with other species. Haigler (*op. cit.*) conducted experiments to determine the mechanism of boring in *Polydora websteri*. She made the remarkable discovery that when the heavy spines of setiger 5 were removed the worm could still bore. She further determined that larvae and post-larvae could bore if the setae and special glands were removed. If this seems to put to rest the idea that the spines of setiger 5 are responsible for boring, then the discovery of Evans (*op. cit.*) that *P. concharum* bores along most of its body is the final blow.

Evans (1969) found that *Polydora concharum* constructs long branching burrows quite unlike those of *P. ciliata* or *P. websteri*. He determined that all branches of this burrow system were being enlarged at the same time. It seems unrealistic to think that the worm could move its body from here to there so as to position the 5th segment to bore.

Based on the results of Haigler (1969) it would appear that the mechanical theory of boring has finally been put to rest. Although she has shown that the spines of setiger 5 are not needed by *Polydora websteri* to bore, it would be of considerable interest to learn what function they do perform. Indeed, the great degree of variation seen among species of *Polydora, Boccardia,* and *Pseudopolydora* of these setae suggests that each species has subtle differences in behavior which have manifested themselves over time in morphological diversity.

Perhaps it is as Söderström (1923) suggested, that the spines are merely used for anchoring the animal in position so that normal functions of respiration and feeding can take place. Why, then, have such species as *Boccardia columbiana, B. berkeleyorum* and *Pseudopolydora reishi,* all of which bore, evolved heavy spines which have the ends formed into brushes? These suggest some mechanism for maintenance of the general well-being of the tube, by cleaning.

Comparative Aspects of Burrow Structure among Species of *Polydora*

The U-shaped burrow, typical of *Polydora* shell infestations, assumes different shapes and forms among different species.

The simplest burrow is formed by *Polydora commensalis* which occupies hermit crab shells. The worm excavates a shallow depression and roofs it over with a thin calcareous layer (Figure 3c) (see earlier discussion and Blake, 1969a). The same type of burrow has been found for *P. bioccipitalis* by Blake & Woodwick (1971b). Both species form their burrows near the shell opening and on the columella.

The "typical" U-shaped burrow is formed by *Polydora ciliata* (Figure 3d). *Polydora websteri,* however, modifies the basic U pattern in several manners.

1) The U twists (Figure 3g) as in *Mercenaria mercenaria* infestations (Landers, 1967);
2) The U expands at the base and may be inflated, the shape assuming a "pear-shape" (Figure 3e);
3) The U may have a single branch at the bottom (Figure 3f) as in *Placopecten magellanicus* (Evans, 1969).

Polydora websteri also forms mud-blisters in oysters. Pear-shaped burrows have also been reported for *P. hoplura* by Korringa (1951).

The greatest deviation from the U pattern is the multiple branched burrow described by Evans (1969) for *Polydora concharum* in *Placopecten magellanicus* (see also earlier discussion). Here the burrows branch repeatedly (Figure 3h). Such burrow patterns are difficult to trace without X-Ray techniques (Figure 4). Similar burrows occur in other species, such as *P. convexa* (Blake & Woodwick, 1971b).

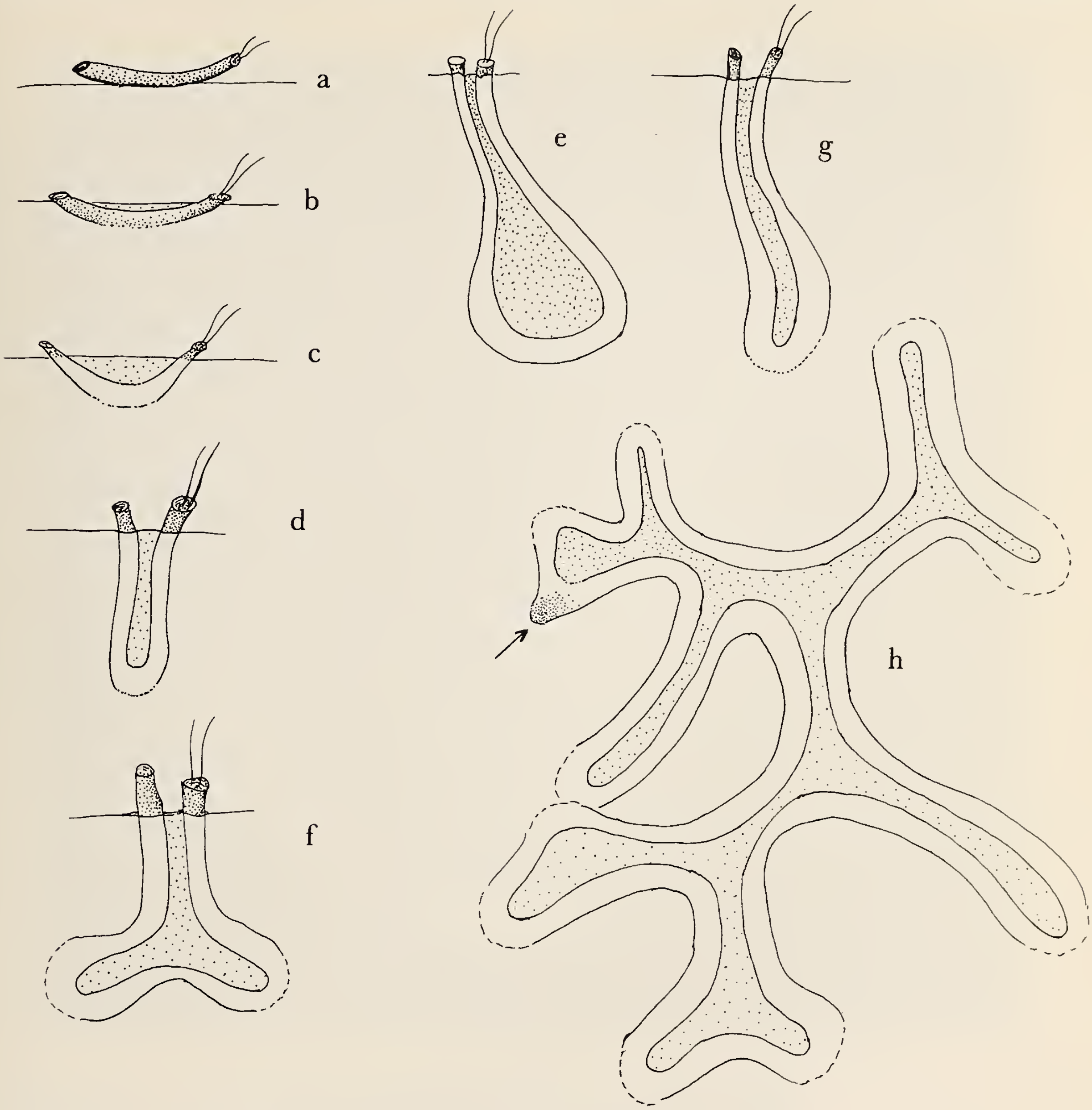

Figure 3

Diversity of burrow structure in *Polydora* species

a: tube of just settled larva; b: initial boring activity of worm, this is the stage reached by *Polydora commensalis;* c: continued boring; d: U-shaped burrow such as that formed by *Polydora ciliata*; e: pear-shaped burrow formed by *Polydora websteri*; f: single branched burrow formed by *Polydora websteri* in *Placopecten* shells; h: multiple branched burrow of *Polydora concharum* from shells of *Placopecten magellanicus* (after Evans, 1969)

Figure 4

X-ray photograph of the upper valve of *Placopecten magellanicus*. Multiple branched burrows of *Polydora concharum* are clearly evident in the center of the shell, while the smaller burrows around the periphery are mostly those of *Polydora websteri*

Dependence of Polydorid Species on a Calcium Carbonate Substrate

A survey of the habitats of all known species of *Polydora, Pseudopolydora,* and *Boccardia* (Table 5) reveals that 26 species have been reported to occur only in calcareous substrates; 6 from both calcareous and non-calcareous substrates; 33 from various non-calcareous substrates; and 5 in which the exact habitat is not known.

The most often reported species, *Polydora ciliata* has been reported from both calcareous and non-calcareous substrates. The literature, however, is confused to say the

Table 5

Habitat Records of the Known Species of *Polydora, Boccardia* and *Pseudopolydora*

A. Species which occur exclusively in calcareous substrates	
Polydora alloporis	*P. maculata*
P. anophthalma	*P. pacifica*
P. armata	*P. pygidialis*
P. bioccipitalis	*P. tetrabranchia*
P. capensis	*P. websteri*
P. commensalis	*P. wobberi*
P. concharum	*Pseudopolydora corallicola*
P. convexa	*Ps. pigmentata*
P. elegantissima	*Ps. reishi*
P. giardi	*Boccardia berkeleyorum*
P. hoplura	*B. columbiana*
P. hornelli	*B. pseudonatrix*
P. langerhansi	*B. tricuspa*
B. Species reported from both calcareous and non-calcareous substrates	
Polydora socialis	*P. flava*
P. ciliata	*Boccardia hamata*
P. caeca	*B. proboscidea*
C. Species which occur exclusively in non-calcareous substrates	
Polydora abranchiata	*P. nuchalis*
P. aggregata	*P. paucibranchus*
P. anoculata	*P. quadrilobata*
P. cardalia	*P. rickettsi*
P. caulleryi	*P. spongicola*
P. cirrosa	*Pseudopolydora antennata*
P. citrona	*Ps. kempi*
P. colonia	*Ps. paucibranchiata*
P. fulva	*Ps. pulchra*
P. goreensis	*Boccardia basilaria*
P. laticephala	*B. chilensis*
P. ligni	*B. ligerica*
P. limicola	*B. natrix*
P. magna	*B. perata*
P. neocardalia	*B. polybranchiata*
P. normalis	*B. proboscidea*
	B. truncata
D. Species in which the exact habitat is not known	
Polydora hartmanae	*P. posthamata*
P. hermaphroditica	*P. saint-josephi*
P. heterochaeta	

least. It is probable that a majority of the records attributing *P. ciliata* to non-calcareous habitats actually refer to *P. limicola* Annenkova, 1937, or *P. ligni*. The literature also seems somewhat confusing with regard to *P. caeca* and *P. flava*. Both species have been reported from calcareous and non-calcareous habitats from widely scattered areas of the world. It seems possible that other species such as *P. concharum* may actually refer to some of these records. Considerable work remains to straighten out the taxonomic status of several of the "better known" species of *Polydora*.

NOTE ADDED IN PROOF

The paper by Mohammad (1972) arrived too late to be incorporated in the text and tables of the present paper. This work includes the original description of *Polydora vulgaris* from the Pearl Oyster, *Pinctada margaritifera* (Linnaeus, 1758). Also included is information of the form of the burrow and rates of infestation. He indicates a total of 4.68% *Pinctada margaritifera* are infested with *Polydora vulgaris*. Infestation is higher in older oysters (14.77%), in those with pearls (19.43%) and highest in old pearl carriers (41.2%).

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